

The early evolution of the plant life of South-western Australia*

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Abstract

A general review is given of the evolution of plant life in Australia, with special reference to south-western Australia where the evidence permits, from the beginning of life on Earth to the end of the Cretaceous, at which time recognizably modern floras had come into existence. Western Australia comprises the whole span of life as it has fossil stromatolites of the earliest known, 3 500 million years old, and living colonies of stromatolites at the present day. Only very primitive forms of life existed until the Cambrian, 570 my ago; land plants first appeared in the Upper Silurian (400 my) and became well established in the Devonian (395-345 my). An accurate impression of the plant life in Western Australia in the Lower Permian (270 my) can be formed due to the abundant remains in coal deposits when the *Glossopteris* flora of seed ferns was dominant.

Development of higher forms of life continued into the Mesozoic Era (225-65 my) with rising temperatures and climates at first arid and then humid tropical. Cycads and cycad-like plants, and gymnosperms ancestral to modern southern conifers — kauri pines, podocarps and Araucarians — became dominant but were superseded by the flowering plants (Angiosperms) during the Cretaceous (135-65 my).

Following a discussion of the origin of the Angiosperms, I suggest that colonization of Earth by plants was not immediate but gradual. At the outset, relatively primitive plants could grow only in wet places but gradually more difficult habitats could be colonized. It is argued that even so it was only with the coming of the Angiosperms with their greater evolutionary plasticity and ability to adapt to adverse habitats, that the entire surface of the earth could be colonized for the first time and a complete plant cover established.

Introduction

Much has been written and much discussion has taken place about the evolution of the plant life of SW Australia, encouraged by the numerous special characteristics which the present-day flora possesses, but this interest has been devoted largely to the later stages subsequent to the appearance of flowering plants during which the present-day flora came into being. This paper attempts to fill in the picture by an account of the early times during which plant life on Earth first appeared, adapted, and gradually colonized the earth's surface.

The history of the vegetation of the Australian region as a whole has been addressed in two recent books by Smith (1982) and White (1986). The first comprises a collection of five papers prepared for the International Botanical Congress in Sydney. The second book gives the whole history of the evolution of Australian vegetation in a well illustrated book. The story told is not without its difficulties and inconsistencies, due to the uncertain evidence and conflicting theories.

The formation of Earth is generally accepted to have taken place between 4 500 and 5 000 million years ago. Just how or when life on earth originated is not known, but fossil evidence of very primitive forms of life has been detected in

rocks as old as 3 500 my. It is a strange fact that for the next 3 000 million years after that — an extremely long period — these forms of life underwent only a very slow development, and it was not until the geological period known as the Cambrian which began around 570 my ago that the evolution of life really got under way.

This horizon was originally chosen for the starting point of the Cambrian period and also for that of the whole Phanerozoic Eon (which means the period of visible life) because it is the point at which readily identifiable fossils appear. It was originally thought that earlier rocks were devoid of evidence of life on earth. With subsequent work it is known that humble forms were in fact there and slowly evolving. None the less it appears that at the opening of the Cambrian period a critical threshold was crossed, beyond which abundant life began to be possible.

Earth in Precambrian times was very different from today; the atmosphere was of very different composition, some say it consisted largely of methane and ammonia (Echlin 1966), others say water vapour, carbon dioxide, nitrogen and various sulphurous gases (Cloud 1968). They agree that it contained little or no free oxygen. Oxygen is vital to the functioning of life, and it is interesting that the supply of oxygen on which life depends had to be built up gradually by the action of life itself. The process of photosynthesis by which plants support their life processes, drawing energy from sunlight to combine carbon dioxide and water into sugars and higher compounds, involves liberating an excess of oxygen from these molecules.

* Presidential address 1987, delivered 22 July 1987.

For a very long time most of the oxygen produced in this way would have been absorbed again in the oxidation of iron and other surface minerals, a stage that may have lasted 2 000 my, but later the photosynthesis of primitive organisms gradually increased the free oxygen content of the atmosphere. Prominent among the early forms of life were the Cyanobacteria or Blue-green "Algae" whose colonies trapped sand and silt and form those curious structures known as stromatolites which we can still see today at Shark Bay (Fig. 1). Stromatolites have been detected in the early fossil record, and Western Australia can claim the oldest known deposit, at the locality "North Pole" in the Pilbara, 3 500 my old. By the beginning of the Cambrian it is supposed that the oxygen content of the atmosphere may have reached a critical level of perhaps 1% (whereas it is 20% today), permitting the evolution of life to progress more rapidly. In the words of Plumstead (1969): "When Phanerozoic time commenced 600 million years ago, the world stage was set for the great biological drama about to be enacted on its surface."

The Palaeozoic Era

At first, the developing forms of life which become abundant in the fossil record are found virtually only in marine deposits, and another 150 million years had to pass, until the oxygen content of the atmosphere had increased still further to perhaps 10%, before indisputably terrestrial vascular plants appear. One reason for this may have been that the early atmosphere, with its lack of oxygen, possessed little or no ozone layer to buffer harmful incoming radiation, so that early forms of life could only have survived under a protective cover of water at least 5m deep (Plumstead 1969).

It used to be tacitly assumed (eg Plumstead 1969) that as aquatic plants came first in the fossil record, land plants evolved from them by adaptation to sub-aerial conditions. Plumstead suggested that land plants evolved gradually at the margins of the sea or other large bodies of water, adapting the ability to survive short periods and even seasons of low water level, until complete adaptation occurred. Even then for a long time early land plants must have had to grow with their roots in water, as their tissues were not sufficiently evolved for efficient uptake and conductance of water, and they could not tolerate desiccation (Plumstead 1969).

More recently this has been questioned by Stebbins & Hill (1980) and others who suggest that large land plants evolved from unicellular soil algae independently of multicellular aquatic plants. If the new suggestion is true, the evolutionary process may have commenced in the Cambrian or earlier, and in fact some fossils found in the Middle Cambrian of Queensland have been claimed to represent land plants (Fleming & Rigby 1972). The occurrence of spores in the fossil record appears to document colonization of the land by non-vascular plants as early as the Ordovician (Gray 1985), but it is not until the Late Silurian about 410 my ago that we find megafossils definitely interpretable as land plants. Whether they evolved from aquatic plants or independently, terrestrial plants can be distinguished by the morphological characters needed to fit them for sub-aerial life, and generally if fossil plants possess cuticle, stomata or lignified vascular tissue they are assumed to be terrestrial.

During the Devonian period, 395 to 345 my, there was a rapid radiation of vascular plants, and it is possible to identify lycopods, ferns, pteridosperms (fern-like plants which were large woody trees and probably seed-plant ancestors), and



Figure 1 Living stromatolites on the shore of Shark Bay (White 1986).

possibly even the earliest seed-plants themselves. It has been suggested that this was an "experimental" phase of evolution, a time when evolution ran riot as innovators flourished in the largely unoccupied ecospace (Runnegar 1982). Except for the Angiosperms which did not appear in identifiable numbers until the Cretaceous, all the extant phyla of plants appeared together very early and were established if not during the Devonian, at least by the Carboniferous. All the same there is a definite progression in time of dominant plant forms, the simpler and more primitive being the more abundant in the early stages, and progressively more advanced forms becoming dominant later. The flora consists predominantly of relatively primitive forms such as lycopods in the Devonian, of ferns and seed-ferns in the Carboniferous and Permian, of gymnosperms by the Jurassic.

The earliest period in Western Australia for which adequate data show what the landscape and its vegetation really looked like is the Permian, 280 to 225 my ago, for two reasons: there is an exceptionally large amount of fossil material, and the geological events of that time have left some traces still recognizable in the landscape. At the outset of the Permian, Australia still formed part of a great continental landmass, Gondwana, from which the separate continents of today would later one by one split off, and it occupied a polar position.

To find the pole of those days one must resort to palaeomagnetic data which are confusing for Gondwana. However, a position for the Permo-Carboniferous South Pole was given by McElhinny & Embleton (1974) where readings from South America, Africa and Australia agree within a reasonable framework of confidence in placing it in the vicinity of Tasmania. Subsequent to the Permian the pole gradually moved away from Australia to its present position.

During the Sakmarian stage of the Early Permian, in keeping with the continent's polar position, the continental shield area of Western Australia was extensively glaciated. The sedimentary basins which surround it — the Perth, Carnarvon, Canning and Officer Basins — contain sediments dated to that time which are of glacial and fluvio-glacial origin. The widespread occurrence of these sediments indicates that the higher land was covered by a continental ice-sheet similar to that of Antarctica today, and the traces left indicate too that the country was extensively abraded by the ice. To form a picture of the landscape after the withdrawal of the ice-sheets one can refer to Québec and Labrador and Finland, where there is country of comparable geological structure based upon ancient crystalline rocks, which has been quite recently glaciated. Such country is of comparatively low relief, scoured into a structure of boss and hollow, and with the hollows now occupied by strings of long narrow lakes showing the direction of ice movement.

The nature of the plant cover in the early Permian of WA is shown to us by the fossiliferous coal beds which were laid down after the withdrawal of the ice, not only in the well known Collie Basin where the coal is mined commercially today, but in the Perth and Canning Basins also, in the eastern States and in other parts of Gondwana. The local plant macrofossils have been described by White (1961) and Rigby (1966) and demonstrate the presence of the "*Glossopteris* flora" which was widespread in the Southern Hemisphere at this period. An artist's reconstruction of it was published as a frontispiece to Plumstead (1969). While this illustration is from a South African source, Africa and Australia formed part of the same continental land mass in those days and shared the same flora.

The immense coal deposits laid down during the Permian are being exploited today both here at Collie and in the eastern States. The stereotype of coal swamps being steamy tropical swamp-jungles, as was the case in the northern hemisphere

during the Carboniferous, is not applicable to southern Permian coals. These coal deposits are the product of cold, swampy bogs in which Horsetails grew in immense profusion like rushes. Ferns and seed-ferns, and probably mosses as in modern peat, as well as herbaceous lycopods like *Selaginella* formed a low, dense, swamp vegetation. Trees and shrubs of the Glossopterids, with special aeration tissues in their roots suited to the boggy conditions, grew in the swamps and in adjacent areas with high water tables (White 1986).

It is impossible to reconstruct accurately the vegetation of any past period because relative abundance of species, dominance and structural features of vegetation cannot be known. One can only depict some typical plants whose form is known from macrofossil remains. The *Glossopteris* flora has been so named because that form-genus is the commonest element. Seven "species" have been identified in Western Australia and constitute 25% of all known macrofossil taxa of that period. *Glossopteris* is a name originally attached to fossilized leaves thought (at first) to represent a fern. Further study has shown that these plants are actually a diverse group ranking taxonomically more at the level of an Order according to White (1986). Glossopterids as they should preferably be called were trees (Fig. 2) with large tongue-shaped leaves up to 40 cm long which were deciduous in the cold winters, so that great mats of them have been preserved where they fell and were stratified in the swamp. The wood had annual rings and secondary thickening, and resembled modern *Araucaria*. Roots had a segmented internal structure which probably had an aerating function. Most interesting of all, the leaves bore various kinds of fruiting bodies which bore seeds, and may well have been the ancestors of later groups of plants such as the southern conifers, the cycads and even the angiosperms.

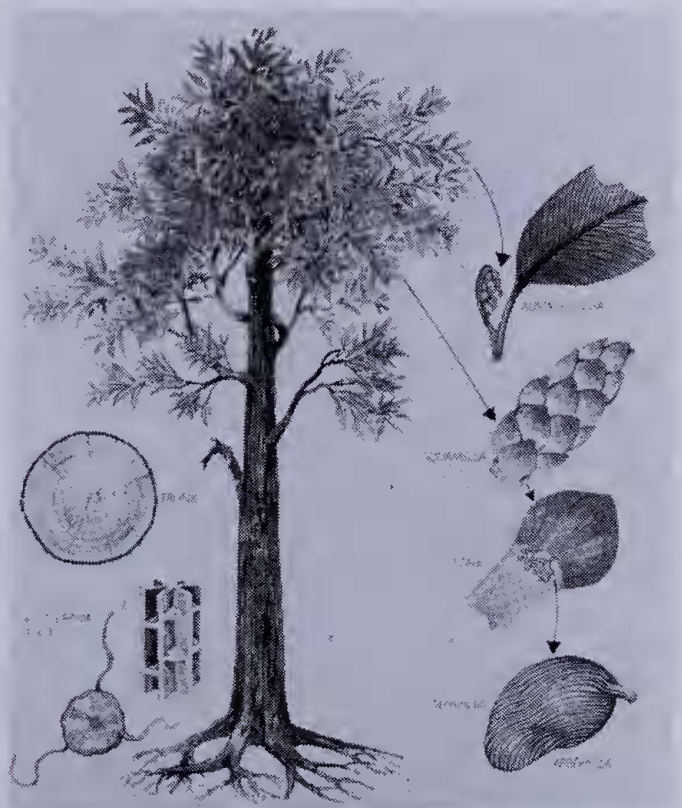


Figure 2 A *Glossopteris* tree with details of leaves, inflorescences, stem and roots (from White 1986).

The Lower Permian macrofossil record shows us vegetation of low-lying and swampy areas. What then was the vegetation of the much greater areas of upland? Did it exist at all? At that epoch most plants were still of a low grade of organization, eg mosses, hepatics, ferns, seedferns, whose modern descendants mostly inhabit wet places. Could they have colonized dry stony uplands in a cold post-glacial period? The answer is to be sought in high latitudes of the Antarctic today where we find communities of bryophytes, lichens and ferns.

A number of different cryptogam tundra communities have been described from the maritime Antarctic by Gimingham & Lewis Smith (1970) composed in order of abundance of the following classes of organisms: lichens, mosses, algae, hepatics, fungi, bacteria, and a few flowering plants. Considerable areas of low-lying ground may become free of snow in summer, a large number of habitats are available for cryptogam colonization, and water is locally plentiful during the short growing season. It is likely that these conditions prevailed also on our uplands in Western Australia during the immediately post-glacial Permian, and that the land was therefore occupied by similar cryptogam communities, while the *Glossopteris* forest occupied sheltered and low-lying places. A similar juxtaposition prevails today in Tierra del Fuego, with subantarctic tundra communities on higher ground, side by side with dense rain forests of *Nothofagus* on protected sites. The point here is that the cryptogam vegetation is able to tolerate cold but not drought. It must have sufficient moisture during the growing season.

The Mesozoic Era

Following the Permian the ensuing era of the Mesozoic spanned 160 my and is divided into the Triassic, Jurassic and Cretaceous periods. The fragmentation of Gondwana took place then (Owen 1983). The portion which is now Australia began to separate on the west from Greater India at the end of the Jurassic (Heitzler *et al* 1973) and from Antarctica during the Cretaceous (Owen 1983). Australia moved steadily towards the equator and experienced a warming of climate, much greater than could be expected merely from the equatorial movement. In the Jurassic and Cretaceous the global picture is of very widespread tropical conditions associated with a progressive warming of the entire earth. The Jurassic period is found to have been already warmer than the present, and by the end of the Cretaceous temperatures had risen to a maximum which according to Hughes (1976) was probably the hottest experienced at any time since land plants first appeared. Subsequently during Cainozoic time global temperatures have been progressively falling away from this maximum until glacial phenomena have once more appeared (Kemp 1978) and the earth has regressed to conditions approaching those of the Permian period.

Evidence for this is based primarily on the past temperature of the sea which is calculable for example by the well-known oxygen isotope determinations from belemnites which give apparently high values generally for Cretaceous seas and much higher temperatures than now in high latitudes (Lowenstam 1964). Hughes (1976) also cited the widespread carbonate sedimentation of the late Cretaceous which he attributed to high ocean temperatures, and pointed to the geographical distribution of certain types of pollen in the fossil record, eg *Classopollis*, as indicating that the equatorial belt was at least 80° of latitude wide (40° on each side of the equator). Under such conditions warmer temperatures would have prevailed in high latitudes as well with absence of glaciation and of polar ice caps. At a number of localities in both hemispheres which were situated at high latitudes in the Cretaceous, often between 70° and 80° from the equator, well within the polar regions, the fossil record shows luxuriant forests of warm-temperate

type, (eg West, Dawson & Hutchinson 1977 for the northern hemisphere, Douglas & Williams 1982 for the southern) and it is difficult to account for this unless the climate of the earth was radically different in late Cretaceous and early Tertiary time.

Various causes can be suggested to account for the situation, the most plausible being either variation in the amount of energy received in the earth's atmosphere, or variation in the tilt of the earth's axis relative to the plane of the ecliptic.

The principal difference between these two mechanisms would lie in the effect at high latitudes. With the obliquity as it is today and a higher solar output, it would be much warmer than now but there would still be seasonal variation in day length and continuous high illumination at high latitudes during the summer months only. With null obliquity there would be no seasonality, no summer or winter, no variation in day length but a low level of illumination, due to the low angle of the sun, during daylight hours throughout the year. Evidence from the late Cretaceous-early Tertiary vegetation of the Canadian high arctic (West, Dawson & Hutchinson 1977) supports the radiation hypothesis. The fauna, which included large land tortoises and alligators, indicates a frost-free climate, whereas the flora was deciduous and petrified wood shows well-marked annual rings indicative of seasonal growth. Furthermore there is an unusual leaf gigantism, inferred from modern studies to be a response to continuous photoperiod (Choi, Traverse & Hickey 1980). These facts appear to disprove any variation in obliquity. Australian evidence from an early Cretaceous flora of Victoria which lay at more than 70° south at that time (Douglas & Williams 1982) shows a similar warm-temperate fauna and flora, although in this case leaf gigantism has not been reported. Axelrod (1984) showed that it would be quite possible for mesothermal plants and animals to tolerate the light conditions and seasonality prevailing at high latitudes at the present day provided much more warmth were available.

Throughout the Mesozoic, therefore, climate was progressively changing, and at the same time the evolution of the Western Australian landscape continued, evolving from the glaciated landscape of the early Permian to a base-levelled landscape which we may call the Gondwana surface and which was perfected by the close of the Cretaceous. King (1972) recognized a series of erosional surfaces in Natal resulting from episodic continental uplift, the oldest of which is the Gondwana surface and is held to be a surviving portion of the surface of Gondwana as it was before rifting and separation. In South Africa the Gondwana surface has been uplifted to 3000m above sea level and most of it has been destroyed by erosion. In Western Australia it has been uplifted less than 300m and is visible as the Yilgarn Plateau, in the interior behind the Meckering Line, where it has remained substantially unmodified since at least the Eocene (Mulcahy 1967).

The fossil record shows us something of the evolution of plant life in response to all these changes. Whether Western Australia remained sufficiently humid in the Triassic for conjectural tundra vegetation of the early Permian to survive, is not known. The likelihood is that it became extinct with the warming and drying of the climate. We cannot be certain whether anything replaced it, because the macrofossil record is probably not showing us the upland flora, while with pollen material we cannot be certain what it represents nor where it came from. White (1986:97) wrote confidently that by late Permian times the drier hillsides and places away from permanent water were habitats for early conifers, Ginkgos and cycad-ancestors, but there is little evidence for this assertion. Microfossils are evidence for the existence of this flora but not for where it grew. An ecologist must examine the likely capabilities of the contemporary plants before making a guess

at their habitat and in this case it seems that they may well have been confined to river plains and other damp places upstream, and did not necessarily grow on hillsides.

Retallack (1977) dealt with the Triassic vegetation of eastern Australia. There is much more fossil material than in the West and Retallack adopted a new approach, treating the eleven different fossil plant assemblages which he found as plant associations in the modern sense, giving them names in Braun-Blanquet terminology, eg *Dicroidietum odontopteroideum*, and inferred habitats. Much of this may appear frankly far-fetched and fanciful. Seed-ferns such as *Dicroidium* (Fig. 3)



Figure 3 Reconstruction of *Dicroidium*, leaf and inflorescences (White 1986).

were dominant in most of the eleven associations, but one was a coniferous forest dominated by *Voltziopsis* a podocarpaceous conifer resembling modern *Dacrydium* (not to be confused with *Dicroidium*). Retallack took the view like so many other palaeobotanists that because terrestrial flora existed it necessarily occupied all habitats and formed a universal plant cover. I find this view hard to support. Retallack confidently drew several landscape diagrams showing the distribution of his hypothetical associations, making them extend to the tops of the hills, and asserting equally confidently that they grew up to 200 km inland from the coast of that time (Fig. 4). White (1986) says of this period that the conifers "grew on dry hillsides, remote from water", but how does she know? Careful reading of Retallack's paper shows no evidence that any association grew on a site where water was not plentiful, and I regard the existence of an upland flora as not proven.

During the ensuing Jurassic period in Western Australia the flora comprised as before lycopods, horsetails, ferns and seed-ferns, but dominance was assumed by gymnosperms. Many of these were cycad-like plants such as *Pentoxylon*, (Fig. 5) and others were coniferous trees belonging to those groups of southern conifers which still survive today, the Podocarps, Araucarias and Kauri Pines (*Agathis*), as well as *Ginkgo* of which a single species survives in China. Here for the first time we begin to find a vegetation which is recognizable in modern terms. A beautifully preserved Jurassic flora is found in the Talbragar Fish Beds of northern New South Wales which were laid down in an ancient lake and show us a forest of kauri pine interspersed with podocarps, and with *Pentoxylon* in the understorey. This is particularly interesting because relict *Agathis* forests on the Atherton Tableland have Podocarps growing among the Kauri Pines and a tree-like cycad, *Lepidozamia hopei*, is present in the understorey. Thus a modern assemblage of plants exists with the same basic composition (though at a more evolved stage). White (1986) claimed from this that "we know exactly what the Jurassic vegetation looked like". At least, we know what some Jurassic vegetation looked like. The Talbragar flora is likely to have grown under cool, constantly humid conditions as its modern counterpart does and cannot be assumed to have formed a universal cover extending over less favourable habitats.

This gymnosperm-dominated flora persisted through to the middle Cretaceous after which it was superseded gradually by a flora of angiosperms (that is, of flowering plants) of modern type and the earlier forms became extinct. This radical biological change was accompanied apparently by an increase in the number and variety of insects and birds, and their co-adaptation as pollinators with the developing angiospermous plants, by the radiation of mammals and the extinction of dinosaurs, not with precise contemporaneity but within the 70-million year timespan of the Cretaceous period. This period therefore witnessed a biological revolution as profound and important as that of the Cambrian when higher forms of life "suddenly" radiated in the sea, and transcending that of the Devonian when the first land plants evolved.

The appearance and early development of the angiosperms occurred from the Barremian to the Cenomanian stages of the Cretaceous and is usually described as "sudden", but actually spanned about 20 million years.

The flowering plants or angiosperms possess a whole range of well-marked characters readily recognizable even in fossil form which distinguish them from their precursors. In addition to their entirely new and distinctive reproductive system, they possess large reticulate-veined leaves, wood with vessels, and distinctive pollen. The earliest of this pollen, in an early and simple form, appears in the Barremian and radiates into more common and complex types by the Cenomanian (Wolfe, Doyle & Page 1975, Fig. 6). The earliest known fruits and seeds are Barremian, while leaves become generally recognizable in the Albian. The earliest known angiosperm remains are found in western Gondwana, and we have no records within Australia until the Albian.

The origin of these angiosperms is unknown. They appeared relatively suddenly and apparently already fully developed, leading to the postulate that angiosperms underwent a long previous period of development which failed to register in the fossil record.

The Russian botanist Takhtajan discussed the problem in the English version of his book (1969). Accepting that there is no factual basis for attempts to derive the angiosperms from ferns or other lower forms without a transitional gymnospermous stage, he proceeded to examine all the known



Figure 4 Reconstruction of Triassic vegetation cover at a site in present north-western New South Wales, after Retallack (1977). Communities shown are Phoenicopsetum levee scrub (dashed shading and conical pattern), Dicroidietum flood plain forest (rounded trees and undulating pattern) and Johnstonietum mallee-like woodland (serrated pattern on hillsides). This reconstruction implies total vegetation cover of the land area.

groups of Jurassic gymnosperms, looking for indications as to which might be candidates for angiosperm ancestry. In a sense this approach was unproductive, since it showed that all of them in one way or another, mainly in wood anatomy and the reproductive organs, possessed characters already too advanced along their own evolutionary line, so that they could not have evolved into angiosperm characters. Takhtajan eventually concluded that the angiosperms and their nearest Mesozoic gymnosperm relatives, the Bennettitales, probably had a common seed-fern ancestor as far back as the Carboniferous, although no trace of such an ancestor had been found. Stebbins (1976) wrote that "all we can say at present is that towards the end of the Palaeozoic era the evolutionary line leading to the angiosperms entered a dark tunnel of ignorance . . . and remained there until the angiosperms emerged, fully differentiated, in the early part of the Cretaceous period."

In the 1960s when Edna Plumstead in South Africa was engaged in her pioneer work on the Glossopterids, she suggested that these may have been among the missing angiosperm ancestors. Takhtajan's conclusion would support this but the idea found little favour among most botanists, who were wedded to the concept that the Ranales, with *Magnolia*-like flowers, were the sole ancestral type. Melville of Kew supported Plumstead from the beginning (Melville 1970) and recently (1983) came out strongly in favour, citing morphological evidence which he contended indicates that Glossopterids and Angiosperms "belong to one lineage which extends back in time for 300 million years". Recently White (1986) has given added support to Glossopterid ancestry. While of course the angiosperms must have had ancestors, we cannot satisfactorily identify them in the present state of our knowledge. It seems useful however to discuss further the why and the where of their origin, as it seems to me that certain points have been overlooked.



Figure 5 *Pentoxylon*, a cycad-like plant of the Jurassic. The name is based on the division of the trunk into five stelae which have secondary thickening unlike modern cycads (White 1986).

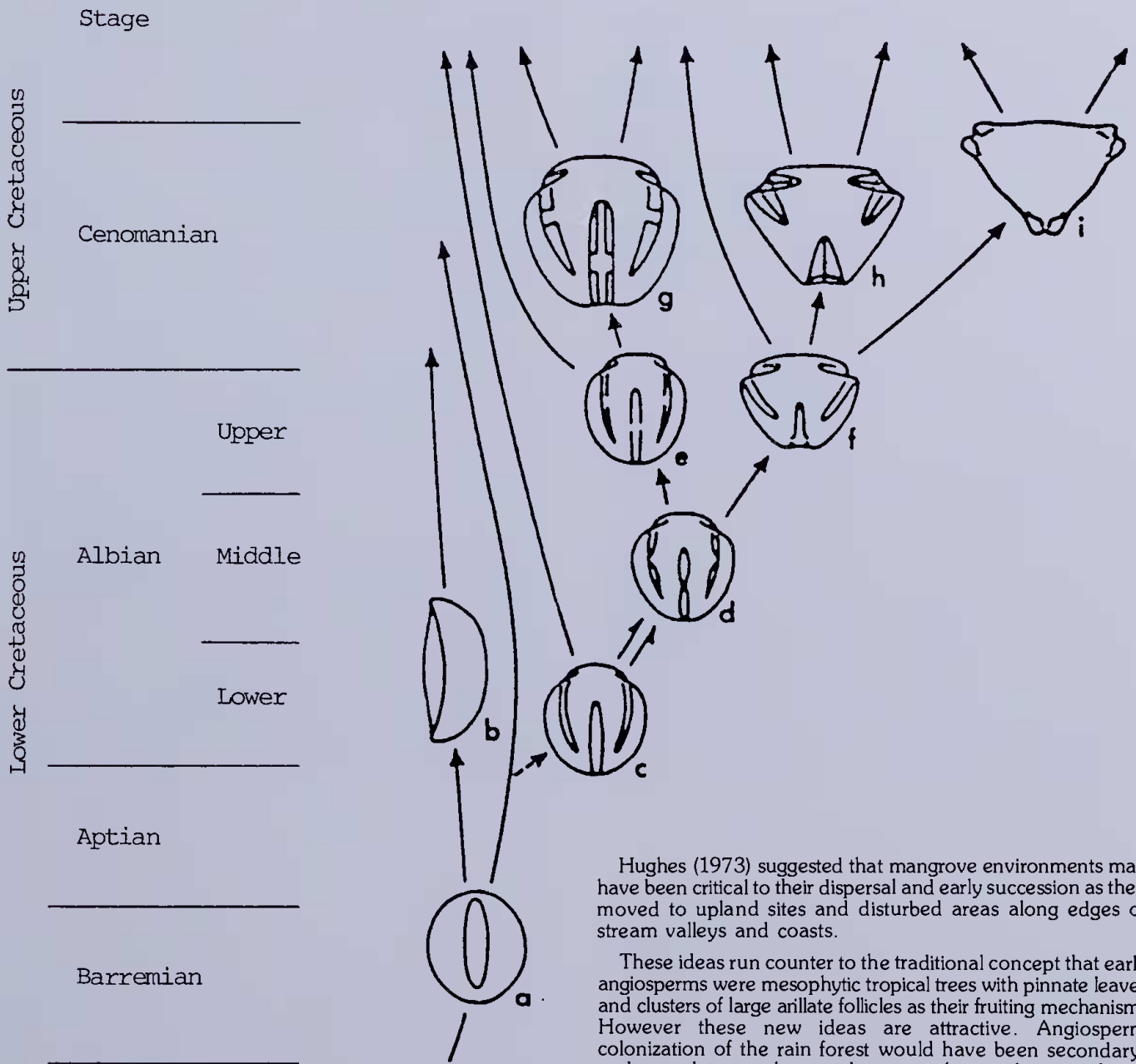


Figure 6 Evolution and radiation of Angiosperm pollen forms during the Cretaceous (after Wolfe, Doyle & Page 1975).

Authors dealing with pre-Cretaceous origins usually follow the "upland origin" hypothesis, whereby angiosperms evolved in rolling hilly terrain and the lower slopes of mountains in the ancient humid tropics. Because these sites were far from the depositional basins, the opportunity for material to become preserved in fossil form would be extremely low except as pollen. Various authors too have speculated as to what the earliest angiosperms were like and what habitats they occupied. On the basis of fossil evidence, the earliest angiosperms may have been small woody evergreen plants with simple, entire, pinnately veined leaves, their flowers pollinated by insects and their seeds distributed by animals (Takhtajan 1969). They may have originated in seasonally arid climates, migrating to more mesic regions later (Hickey & Doyle 1977) initially as riparian weeds or colonists of talus slopes, streambanks and other unstable habitats (Stebbins 1976).

Hughes (1973) suggested that mangrove environments may have been critical to their dispersal and early succession as they moved to upland sites and disturbed areas along edges of stream valleys and coasts.

These ideas run counter to the traditional concept that early angiosperms were mesophytic tropical trees with pinnate leaves and clusters of large anillate follicles as their fruiting mechanism. However these new ideas are attractive. Angiosperm colonization of the rain forest would have been secondary, and come later, perhaps at the stage when we begin to detect them in the fossil record. All of the new hypotheses have in common the concept of initial evolution to fill a vacant niche or niches which would comprise habitats too adverse in one way or another for the more simply organized earlier phyla of plants to tolerate. It seems to me that the logical conclusion of this approach is that it was only with the coming of the angiosperms that something approaching a universal plant cover of the continents was achieved. Even today it is not universal for plants do not grow where the ground is frozen for all or most of the year, or in deserts where too little moisture is available. Before the Cretaceous the range of unoccupiable habitats must have been much greater.

Hughes (1976) is the sole author I have come across who has not assumed that the earth essentially was completely colonized by early land plants in the Palaeozoic and Mesozoic. Hughes observed that if the time from the Devonian period to the present day has recorded progressive degrees of colonization of the land by plants, it follows that many possible habitats now filled would not have been filled in early Cretaceous time.

Support is given to this from a table given by Hughes showing the number of vascular plant taxa existing at various selected moments of geological time. The great diversity of form in the modern flora is expressed in the huge total of 300 000 living species, the great majority being angiosperms. The table shows however that the ferns and gymnosperms have also increased in number since the Cretaceous, having undergone a secondary adaptation to Cainozoic conditions mostly in forms different from those of the Mesozoic. The lower levels of the table give the number of taxa known from the fossil record and it is astonishing to find only 500 taxa of plants in the entire world at the end of the Carboniferous, and 2 500 in the Jurassic. Of course the record is distorted by the selectivity of fossilization, but if the numbers were multiplied by a factor of 10 they would still be astonishingly small.

I am convinced by this that the colonization of the land must have been a long and slow process, not completed before the coming of the angiosperms. I envisage the first small delicate land plants of the Silurian, confined to permanently wet places, perhaps the edges of lakes and ponds. Then in the Devonian and Carboniferous plants increase in size and occupy the deltaic habitats including coal swamps which the fossil record shows us. In the Permian in the southern hemisphere extensive coal swamps were formed and perhaps upland cryptogam communities in a sub-Antarctic climate. In the Triassic and Jurassic as the gymnosperms came to prominence they would first colonize river flood plains and lowlying ground. In the Triassic it is not uncommon to find petrified wood representing rafted tree trunks but these can only have come from the river-bank vegetation ripped away by floods. Trees growing on hills do not get washed down rivers, so that rafted logs are not evidence for upland forests. By the Jurassic, however, gymnosperm forests may have established themselves on favourable upland sites under humid climates, but there would still remain the unfavourable sites, the shallow rocky soils, the steep hillsides, and of course the less humid, hot and dry climates, all of which offered vacant ecospace for the later radiation of angiosperms.

It seems very unlikely that a mere 500 taxa of plants — or even 5 000 — known world-wide in the Carboniferous provided a complete cover for the uplands of the earth. 2 500 taxa or even 25 000 in the Jurassic can only represent a partial cover. The ecological amplitude required of those early taxa would have been far too great. Diverse habitats must have existed then as now, and required diverse adaptations to populate them.

A feature of the angiosperms, and the very basis of their success, is their immense evolutionary plasticity. They evidently radiated quickly in the Cretaceous into a multitude of new and specialized habitats. Ecological diversity is the basis for the great

number of angiosperm species in the world today. This plasticity far exceeds that of the ferns and gymnosperms as we can see from their relative numbers at the present time. Pre-angiosperm floras evolved slowly and lacked capacity to adapt to adverse habits.

This thesis is compatible with the conclusions of others that early angiosperms were small-leaved shrubs or small woody trees originating in dry climates. If "under adverse conditions" is substituted for "in dry climates", these are just the type of plants we should expect to be capable of first colonizing the previously empty spaces of the earth. Further supporting evidence for this comes from the global geological change to predominantly carbonate sedimentation which occurred in the second half of the Cretaceous. Whereas previously sediments had been mostly of erosional origin — sandstones, siltstones and claystones — now they become mostly depositional, *i.e.* limestones, which accumulated from the settling out of calcium carbonate in the skeletons of marine organisms. Hughes (1976) took account of this phenomenon but attributed it to the high temperature of the sea during his "Radmax" period. While this may certainly account for the high quality of the limestone in chalk deposits of that time, we must remember that during the subsequent Cainozoic era carbonate sedimentation has continued to predominate down to our own day even though global sea temperatures have been falling steadily. Other causes have been suggested such as the development of world oceans in the Cretaceous as Pangaea broke up, with their thermohaline circulations and concomitant evolution of calcareous plankton. Such no doubt were contributory but carbonate sedimentation may have been favoured by a reduction in sediment load, resulting in clearer water off shore, and this was the result of establishment for the first time of a general protective plant cover over the uplands. I suggest that by the close of the Mesozoic a general plant cover was more or less established for the first time, by an already ecologically diverse angiosperm flora which had radiated rapidly into a variety of habitats. This flora occupied not only the lowlands, mingling with the Jurassic gymnosperms, but a variety of upland habitats as well.

By the close of the Cretaceous, 65 my ago, there was a fairly general angiospermous vegetation diversified in form from scrub to rain forest, growing in a warm, non-seasonal, humid climate. Since the Western Shield of Australia lay above sea level during the Cretaceous, there is little fossil evidence of the vegetation and we have to rely heavily on data from eastern States sites, supported by local fossil evidence of slightly later date from the early Tertiary. These sources show us a flora whose modern counterparts occur in rain forests of the highlands of New Guinea and New Caledonia, with related types in New Zealand and Tasmania. We can recognize something similar to today's forests of southern beech (*Nothofagus*) and of southern conifers such as *Dacrydium* or mixtures of these, and with other living genera of sub-tropical trees including numerous Proteaceae.

Table 1
Estimated number of seed-plant and pteridophyte species
taxa existing at the selected instants of time (after Hughes 1976)

| Selected instant | Time (my) | Gymno-sperm | Pterido-phyte | Angio-sperm | Approximate total |
|--------------------------------------|-----------|-------------|---------------|-------------|-------------------|
| Recent | 0 | 640 | 10 000 | 286 000 | 300 000 |
| End Cretaceous | 65 | 500 | 2 000 | 20 000 | 22 500 |
| Beginning Cretaceous | 135 | 1 500 | 1 500 | 0 | 3 000 |
| Mid Jurassic (end-Bajocian) | 170 | 1 500 | 1 000 | 0 | 2 500 |
| Late Carboniferous (end-Westphalian) | 300 | 200 | 300 | 0 | 500 |

Acknowledgements I thank Prof B E Balme, Dr A E Cockbain, Dr K J McNamara and Dr G Kendrick for critically reading the manuscript and for their helpful suggestions, and Ms M E White for permitting me to use four illustrations from her book (White 1986).

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